

Reproductive behavior of *Homalonychus selenopoides* (Araneae: Homalonychidae)

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Abstract. *Homalonychus selenopoides* Marx 1891 is endemic to the coastal plains of the Sonoran Desert in the state of Sonora, Mexico and the southwestern United States. Although the species was described more than a century ago, nothing is known about its behavior. We collected spiders in the southern Sonoran Desert to study their reproductive behavior, which we recorded with an infrared camera, mainly at night. Sperm induction was of an indirect type; males wove a triangular sperm web about 2 cm² near the ground. Females and males prepared threads of silk and sand. Courtship behavior was intermediate between levels I and II, and the copulation position was a modification of type III, where the male tied the female's legs with silk before mating. Sexual cannibalism may occur during mating. Females began to spin their egg sac at ~11 days after mating and completed it in ~15 h, including ovipositioning. The outer layer of the egg sac contained sand, and the sac was surrounded by a garniture of cords of silk and sand, possibly to protect the eggs from desiccation and as a barrier to parasites and predators.

Keywords: Sperm induction, courtship, copulation, egg sacs

Homalonychus selenopoides Marx 1891 is endemic to southwestern Arizona and small areas in southern Nevada and California. In México, it occupies the coastal desert plains in the state of Sonora and Isla Tiburón (Roth 1984; Crews & Hedin 2006). Despite its broad distribution, and more than a century after it was first described (Marx 1891), virtually nothing is known about its behavior. This species is included in the family Homalonychidae, which is represented only by the genus *Homalonychus* Marx 1891, including two species. The other species, *H. theologus* Chamberlin 1924, inhabits the Baja California peninsula, extreme southeastern California, and southern Nevada. Homalonychids are cursorial spiders that are not commonly encountered (Vetter & Cokendolpher 2000); they are nocturnal and conspicuous. Adult males are 6.5–9.0 mm, and adult females are 7.0–12.8 mm and are usually found in fine sand or soil and under rocks, wood, or debris. Typically, juveniles and adult females camouflage their bodies with fine soil particles that adhere to the setae of their integument, which allows the spider to blend in with the surrounding soil (Duncan et al. 2007). They are often found slightly buried in the sand with their legs extended (Roth 1984).

Gertsch (1979) mentioned that the family Homalonychidae was enigmatic because very little was known about it. Even now, there are few studies available. Roth (1984) carried out systematic studies of the family. Vetter & Cokendolpher (2000) described the egg sac and defensive posture of *H. theologus*, and Domínguez & Jiménez (2005) reported on sexual and cryptic behavior of *H. theologus*. Crews & Hedin (2006) explained the phylogenetic divergence of the two species and Duncan et al. (2007) described the convergence of *Homalonychus* and *Sicarius* Walckenaer 1847 (Sicariidae) in the morphology of their setae for retaining soil particles. Other studies (Roth 1984; Griswold et al. 1999; Miller et al. 2010) are

concerned only with the systematics or phylogeny of homalonychids.

Here, we describe the reproductive behavior of *H. selenopoides* under laboratory conditions, including sperm induction, preparation of silk threads with adhering sand, courtship and copulation, and spinning of the egg sac.

METHODS

We collected spiders in the bed and sloping sides of the ephemeral stream El Macapul and surrounding area located northern of San Carlos, Sonora (27°59'00"N, 111°02'16"W and 28°00'55"N, 111°03'05"W), in the extreme southern part of the Sierra El Aguaje. The climate is very dry: hot in summer and warm in winter. The mean annual temperature is 22–24°C and the mean annual rainfall is 75–200 mm; summer and winter rainfall is split ~90% and ~10%, respectively (INEGI 1999). Vegetation is desert scrubland with *Bursera* and *Jatropha* predominating (INEGI 1984). Soils are weakly developed and shallow (< 25 cm), usually composed of unconsolidated coarse-textured sand and fine gravel with rocky areas without soil or some soil found in depressions among the rocks (INEGI 2002). The stream bed is almost entirely sand and gravel.

We made 17 diurnal collections with 3–4 participants between October 2007–April 2008. During this period, we captured 186 adult and immature spiders from under stones, dry cattle dung, wood, bricks, or cardboard. We placed each live spider individually in a plastic container and transported all of them to the laboratory in Hermosillo, Sonora, Mexico. Male and female voucher specimens were preserved in 75% ethanol and deposited in the Arachnological and Entomological CIBNOR Collection in La Paz.

We maintained each live spider individually in a 500-ml transparent plastic jar containing 1 cm soil substrate from the collection site and a small container of wet cotton for water. Specimens were initially fed crickets (Gryllidae) and cockroaches (*Blattella* sp.), and later mealworm larvae *Tenebrio* sp.

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(Dominguez & Jiménez 2005). We used mealworms because they are easy to cultivate. The breeding room (3×3 m) was kept at $18\text{--}28^\circ\text{C}$, under natural photoperiod, and 36–60% relative humidity. We observed courtship and copulation in this facility, but made observations of sperm induction and spinning of egg sacs in another small room. We recorded spider behavior with an 8 mm digital camcorder equipped to record infrared light.

Sperm induction.—We placed five males reared in the laboratory and two field-collected males individually in 1750-ml clear plastic jars (13 cm diameter) with fine sand to a depth of 2.5 cm. We added a small flat stone for attachment of the sperm web, as well as an arched cardboard shelter and a small container of wet cotton. From 14 March–14 April 2008 from 20:00–08:00 h, we made momentary observations at intervals of 20 min using an infrared light camera. For these specimens, the ambient temperature was $17.2\text{--}30.7^\circ\text{C}$, natural photoperiod, and 20–47% relative humidity.

Mating behavior.—From January–March 2008, we formed 25 mate pairings with eight adult males and 23 adult females collected in the field (age and reproductive status unknown). Because we had few males that were very variable in their behavior, we used mainly males that were actively searching in these trials; the other males were less active or fled from females. Throughout July 2008, we formed another 20 pairings with 14 males and 12 females reared in the laboratory, (virgins, of known age) plus one female from the field. In these trials, we made these pairings at random, although the males were also variable in behavior. We formed additional mating pairs (one in October 2008 and 18 in July–August 2009) to see if additional behavioral acts had been undetected during the initial pairings; these results were not used in statistical analyses. In all these cases, some females and, more frequently, males were used again to form new pairings. Observation schedules and laboratory conditions were as follows: in January 2008, 14:30–18:00 h, $18\text{--}19^\circ\text{C}$, 50–60% relative humidity; in February 2008, 15:00–20:00 h, $24\text{--}25^\circ\text{C}$, 50–60% relative humidity (temperature was maintained with an electric heater); in July 2008, 20:00–23:00 h, $24\text{--}28^\circ\text{C}$, 36–55% relative humidity. We placed individual females in glass terraria ($20 \times 20 \times 10$ cm) containing a 2-cm substrate of fine sand. We introduced a male 20 to 177 min later (median = 72 min). If the female was receptive, we filmed the behavior and continued filming for 15 min after copulation. We separated individuals or changed their partners if copulation failed to occur within 55 min, or sooner, if they tried to escape, or if an individual repeatedly ran from its partner or assumed a defensive posturing of paired legs. When disturbed, these spiders extend their first two pairs of legs together and forward and the last two pairs together and backward (Vetter & Cokendolpher 2000). In one trial in July 2008, we introduced two males simultaneously.

Egg sac construction.—We used 20 captured adult females, each of unknown reproductive status but with a large opisthosoma, to observe egg sac spinning. These females were captured in the winter of 2008. We placed each female separately in a 1750-ml transparent plastic jar containing a 3-cm sand substrate and one of three types of shelters: 1) an arched piece of cardboard; 2) flat stones glued together with molding silicone; or 3) stones with a glass ceiling. Shelters 2



Figure 1.—*Homalonychus selenopoides* male during loading of sperm.

and 3 had a flat horizontal roof at least 5×5 cm at a height of 2.0–2.5 cm above sand level. We placed five females in these terraria, replacing them every 4–5 days if they failed to spin an egg sac. Observations lasted from 22 April–16 May 2008. Ambient temperature was $24.8\text{--}33.8^\circ\text{C}$, with natural photoperiod, and 16–31% relative humidity. We did not observe or record the spinning of the egg sacs by females that had copulated in the laboratory in July 2008; however, we noticed that each female had produced several egg sacs.

RESULTS

Sperm induction.—We observed the entire sperm induction process once (02:38–03:00 h), when a male wove a sperm web in 5.9 min, close to the sandy substrate; it was slanted and attached to the cardboard shelter and to the wall of the jar. The male stood on the substrate, placed his body on the web, and pressed against it twice. Infrared light failed to show sperm deposition. Subsequently, the male moved a pedipalp in an arch-like motion from top to bottom on one edge of the web to load the pedipalp with semen, rubbing the ventral part of the cymbium against the lower surface of the web (Fig. 1) with soft movements. He raised this pedipalp to carry out the same process with the other pedipalp. So, the semen was deposited on the upper side of the web and it was then absorbed through to the underside. This stage took 7.8 min. The male then climbed off the web and rested on the sandy substrate. The entire induction process took 16.5 min. We also observed the last 2 min of semen loading of another male at 04:28 h, with a position and process identical to the one that we had observed in its entirety. This male then rested on the web for 2.2 h.

Three laboratory-reared males (age 6–8 days as adults) and two field-collected males wove six sperm webs (one in November 2007 and five in March–April 2008). Web dimensions varied from $9 \times 13 \times 15$ mm to $21 \times 26 \times 28$ mm. Webs were triangular, thin, and semi-transparent, with one or several layers of silk (Fig. 2). Webs had two strips of denser sheets that extended from the center to one edge; on this edge, the male arched his pedipalps during induction. The



Figure 2.—Sperm web of *Homalonychus selenopoides*.

webs were set between stone or cardboard and the wall of the jar, inclined at angles of 40–70°, with a height above ground level at their lowest between 2–8 mm and at their highest between 12–24 mm. One male wove two sperm webs, another male wove over a prior web, and two males wove rectangular webs.

We observed variations in form and size of other male webs, but these were not observed during construction. Two males wove triangular ~1 cm-wide sperm webs attached to the top of the container and the mesh. Other males wove webs on the sand that were 1–2 cm long, as short strips that went from “aggregates” of sand and silk from the ground, stuck to the wall of the jar or the cardboard shelters. Some spun elongated silk sheets (~1 × to 5.5 cm) upon sandy aggregates. Other males first wove smaller webs before undertaking larger sperm webs.

Silk and sand threads.—In July 2008, five males placed in glass terraria spun six threads of silk and sand in form of “cords” (Fig. 3). Three threads were spun before and two after copulation, and another was spun without the spider participating in copulation. Males spun threads with their spinnerets, moving slowly with their legs close to their body and constantly touching the thread with their pedipalps. They walked very close to the floor, weaving in the same track two or even five times. The spiders spun threads in 4.7–18.3 min. Four of the threads ranged from ~8.0–17.3 cm, with knobs or swellings at one or both ends. Two threads were 1.9 and 2.4 cm long, with one thick end and the other end bifurcated. We did not observe reactions of females to male threads, because the males approached the female to mate before the females walked on the threads. In July 2009, one female spun threads with silk and sand prior to copulation. The female continuously wove these threads with her spinnerets, leaving a grid of threads on the sand. The threads were very thin in the form of a rosary, but were visible because the sand grains adhered to them. The male placed in this terrarium encountered the female’s threads and immediately began spinning a thread (cord).

Mating behavior.—We observed 16 successful pairings, three in January–March 2008 and 13 in July 2008. Two pairs of

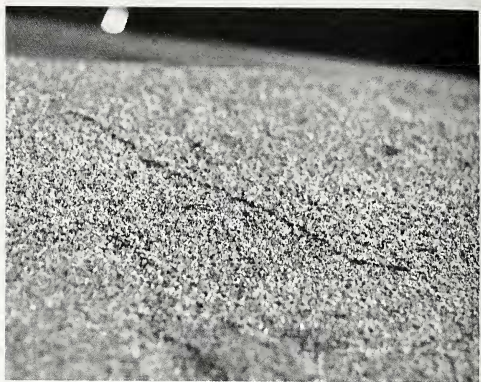


Figure 3.—Thread of silk and sand spun by a *Homalonychus selenopoides* male.

spiders copulated twice; these second matings were not considered in our analysis. Sexual behavior was divided into three stages: pre-copulation, copulation, and post-copulation (González 1989; Domínguez & Jiménez 2005). The sequences of behavioral acts and transition frequencies, including secretion of silk and sand threads, are summarized in Fig. 4.

Pre-copulation: During his search to find the female, the male advanced in what appeared to be a random manner, exploring, walking slowly, and gradually raising and lowering his first pair of legs. The male could also approach the female directly in a targeted manner when he apparently had identified her. In 16 observed copulations, search time prior to mating ranged from 0.1–39.4 min (median = 11.8 min). The initial contact or touch between potential partners was with the tarsi of the forelegs. When the male reached a receptive female, she became passive and he quickly and repeatedly touched and tapped her prosoma, opisthosoma, or legs with the tarsi of his forelegs for ~1–3 s. If the female was initially unreceptive, she could abruptly retreat or walk away. Then the male initiated the courtship. Females also initiated approaches or courtship; then the male could flee or begin tapping or begin courtship. Rejections in form of attacks against consorts were observed only in one pair; the female attacked the male and later the male attacked the female.

During courtship, the male drummed on the ground with his forelegs or with his first two pairs of legs. Legs vibrated when they were in contact with the ground. The left and right legs were extended and moved up and down quickly and alternately. Also, he drummed on the ground slowly and gently with the pedipalps while moving forward or side-to-side. When a female initiated courtship, she approached the male to touch him, then took a “stalking” stance while moving slowly or swiftly with one or more quick approaches. Of the observed pairings, 50% included some period of male courtship. In 25% of the 16 pairings, females approached and touched males. When it occurred, male courtship lasted from < 1–33.5 min (median = 3.1 min) and the female courtship lasted only a few seconds.

Copulation: After a male touched a female, she brought her legs toward her body, leaving the patellae almost touching above the carapace; only the tarsi and metatarsi of the fourth pair of legs were directed backward. The female remained passive and motionless in a quiescent state (Becker et al. 2005). The male climbed onto the body of the female, tapping her with the tarsi of the forelegs and pedipalps anywhere on the body and legs. Then the male climbed up one side or the back of the female and settled on top of the female, facing the opposite direction. During mounting, the male continuously touched the body of the female. Of 16 observed copulations, in seven of the mountings (44%), males approached the females frontally; the other mountings were made from behind or from one side.

While mounted, the male wove threads of silk in circles around the legs of the female to form a broad ring tie, like a veil, covering the exposed surface of the legs, except tarsi and metatarsi of the fourth pair. The male also added sand to the silk on the sides and bottom of the female body as "counter balances." This web is known as the "bridal veil" (Bristowe 1958; Domínguez & Jiménez 2005). While the male was weaving, he was tapping the female's body and legs with his forelegs and pedipalps. The tying was repeated alternately and successively with insertions of the pedipalps (a tying always preceded insertion of a pedipalp).

During insertions of the pedipalps, the male placed the quiescent female on her side, either right or left, moving to that side while he was embracing her with his first three pairs of legs and resting with the fourth pair on the floor. The male's left pedipalp was inserted into the genital opening of the female on the left side while the female was lying on the right side or vice versa. The pedipalps could be alternately inserted, or a pedipalp could be sequentially inserted. During insertion of the pedipalp, the male vibrated his legs II and IV on the same side as the inserted pedipalp. In the 16 observed pairings, the duration of copulation (mounting) ranged from 0.6–9.4 min (median = 1.9 min). The number of pedipalp insertions per mating ranged from 2–12 (median = 2.5); of 85 individual insertions, 66% were done with the right pedipalp and 34% with the left pedipalp.

Successful mating among pairs depended on the origin of the females. Of the 25 pairs formed with the field-collected females in January–March 2008, the successful rate for mating was 12% because only three pairs mated; thus 88% of the females were unresponsive. One female copulated twice with the same male during the same session. On the other hand, the rate of success of the 20 pairs formed with virgin laboratory-reared females in July 2008 was 65%. There were 12 ordinary copulations and one case in which a female presented with two males, mated first with one, then minutes later copulated twice with the other. Five of 12 virgin females received a second or third partner after rejecting the previous male, but finally 100% of the virgin females were receptive. The only pair that included a field-collected female did not copulate.

Post-copulation: Copulation finished when 62.5% of the males dismounted from the females and withdrew, walking away while they remained quiescent for a few seconds. Also, copulation finished when 37.5% of the females were no longer quiescent, extended their legs breaking the bridal veil, and the males fled. Females usually took less than 2 s to break the veil and walk or run, although one female took 16 s and one took 10 min.

After breakout, females rubbed their legs together to remove the remnants of the bridal veil. 38% of the females dug in the ground at least one time, then rubbed and wiggled the back and belly of their prosoma and opisthosoma, and legs in the soil; sand particles then adhered to their body surface. We did not observe this behavior in males. In all pairings, males vibrated their opisthosoma after dismounting; they raised and lowered it with quick short movements. Also, the males cleaned the ventral cymbium of the pedipalps (presumably copulatory structures) with their chelicerae. These actions occurred at least one time in each male and took place within a few minutes after copulation. Males showed post-copulatory courtship in 50% of the couplings. We present the full range of post-copulatory acts and their sequences in Fig. 4.

In January–March 2008, there were two cases where the males were captured and killed by the females within the first 7 min of waiting, without courtship or mounting taking place. When males were killed, their body contents were consumed in the subsequent (undetermined) hours. In January 2008, we observed one event of sexual cannibalism after copulation. In this case, after the last insertion of the pedipalp the female suddenly extended her legs, broke the veil and quickly reached the male as he attempted to escape; all this took place in about a second. In October 2008, there was another event of sexual cannibalism, but this male was caught during mating. In this case, both individuals were lying on the ground, belly to belly in opposite directions, when the female grabbed the male on the ventral side of his opisthosoma. The female broke the veil, broke free of the male for a moment, and caught him. These males were also consumed in the subsequent hours.

In the 22 pairs that did not copulate in January–March 2008, we observed rejection by both males and females, immobility of one or both partners, with or without legs in paired position, and constant attempts to escape from the terrarium. Also, we observed that some males touched or stood on unresponsive females with their tarsi, but apparently the females were not detected. Our waiting time to complete these trials ranged from 22–55 min.

Egg sac construction.—Eight females that copulated in July 2008 started to spin their first egg sacs 9–13 days after mating; spinning was not filmed. Five females collected in the field began spinning their egg sacs, but only four finished. We recorded the spinning of two egg sacs from beginning to end and the other two after the first phase had started.

The female initiated the egg sac construction behavior when she explored the shelter roof; also, she could scratch the sandy substrate. Then she started spinning the egg sac by weaving a silk sheet, thin and circular, on the roof of the shelter. This took 54 and 69 min. Thereafter, she wove thick double strands of silk and sand in the shape of cords. While she was inverted on the ceiling of the shelter, she dropped her opisthosoma and fourth pair of legs grasping the shelter with her three other pairs of legs. With her spinnerets in contact with the sand, the female secreted silk threads and added sand to these in short zig-zag strokes, leaving a cord behind her, which was also folded in a zig-zag pattern. Afterwards, the female raised her opisthosoma and the fourth pair of legs, staying inverted, and attaching to the ceiling the proximal end of the extended cord that was attached to her spinnerets. This process was repeated with other cords to form a first outer circle or ring of the sand-

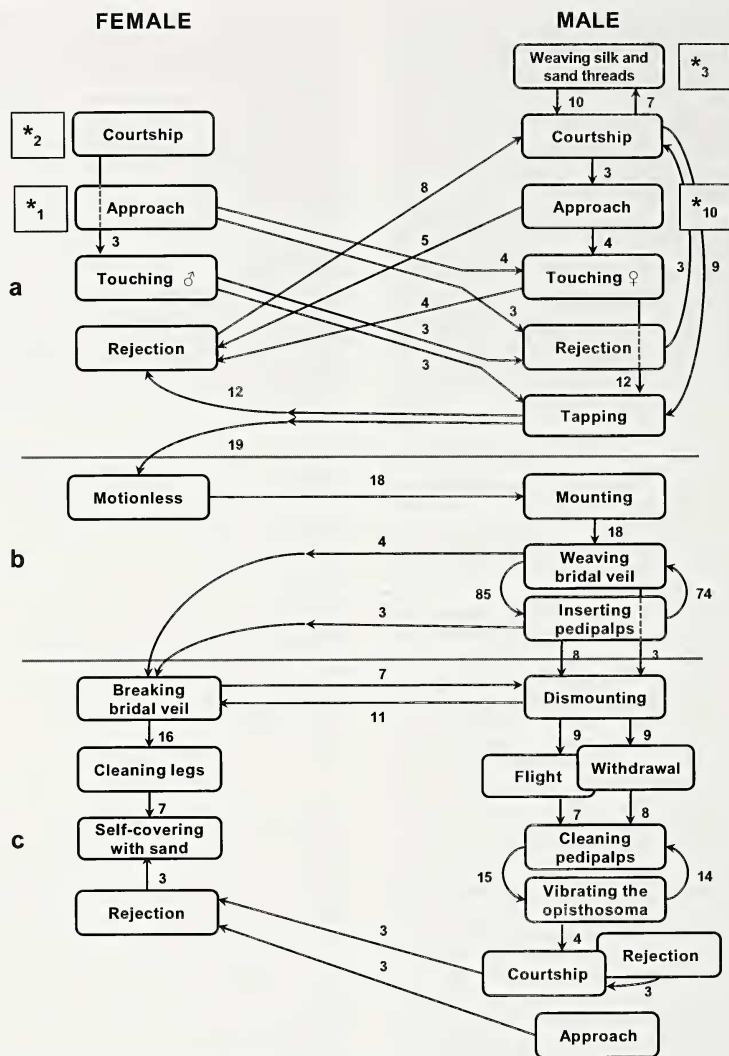


Figure 4.—Sexual behavioral sequences observed in 18 pairings of *Homalonychus selenopoides*. a) Pre-copulatory stage; b) Copulatory stage; c) Post-copulatory stage. The numbers adjacent to arrows represent the total number of transitions. Sequences that occurred one or two times are not included. Asterisks indicate the behavioral acts where a sequence began, and the numbers beside the asterisks indicate the number of sequences that began in these acts.

silk garniture of the future egg sac. During this process, the female was centrally positioned inside this circle (Fig. 5) as she spun silk strands concentrically inward (Fig. 6). The garniture increased progressively in thickness, and the internal space was reduced to include the female only. The female lowered herself

from the shelter at intervals to rest on the ground or to dig and accumulate sand taken from under the shelter.

We inferred that the females lined the interior of the last cord layer circle of the egg sac with silk because the tube walls moved continuously, forming the inner layer of the egg sac.

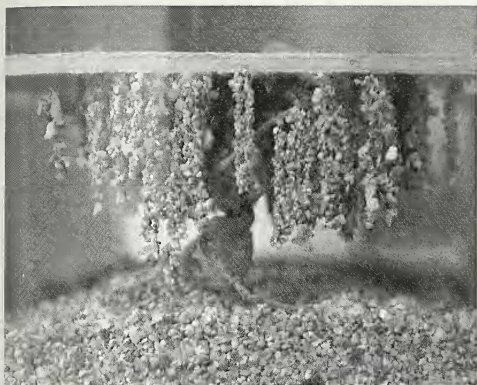


Figure 5.—*Homalonychus selenopoides* female spinning the outer ring of silk cords of the egg sac.

The lower end of the tube was gradually withdrawn and sealed, forming the completed egg sac. Afterward, females were immobile for 5–6.5 h, with only sporadic movements of the tubular wall. We inferred that oviposition occurred during this time. Subsequently, females broke the bottom side of their sacs with their first two pairs of legs to exit. Escaping required 28 s and 10.3 min for two females observed. Immediately afterwards, each female embraced her egg sac and closed the exit rupture with her spinnerets. The other two females were not observed because they were on the opposite side of the egg sacs from where we were filming. It took 14 and 15.5 h from the start of weaving the silk sheet until the females emerged from the sac.

The whole egg sac consists of two sections, a thick exterior garniture of sand-silk cords and the egg sac in the center. The whole structure is shaped like a short cylinder and the egg sac

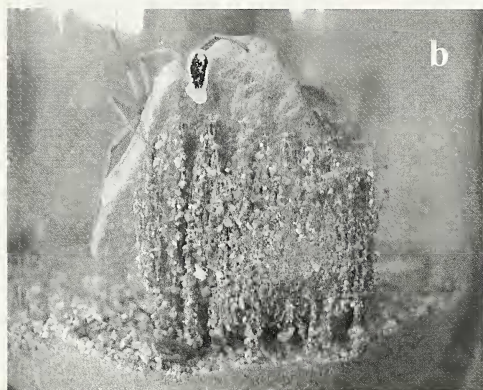
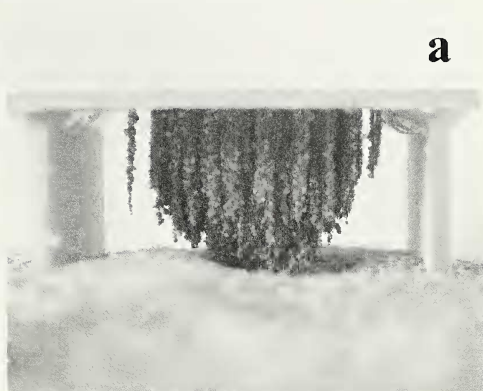


Figure 7.—Egg sacs of *Homalonychus selenopoides*. a) Egg sac spun on a wide, horizontal surface; b) Egg sac spun on a reduced, sloping surface.

can extrude from below, between the garniture of cords (Fig. 7a). Six other captive females also spun egg sacs in the laboratory. One female spun a flattened egg sac under an inclined rock in a very narrow space (Fig. 7b). Later, this female spun two other flattened egg sacs under the same rock. Moreover, in the absence of a shelter, four unobserved females deposited naked eggs directly on the sand surface and the other female also deposited naked eggs on the woven cloth that covered the jar.

DISCUSSION

We observed all stages of reproductive behavior of *H. selenopoides*. Most reports on spider reproduction include only some stages. Sperm induction had not been observed before in the Homalonychidae, and the function of the bridal veil in *H. selenopoides* still remains obscure. Apparently, adding sand to

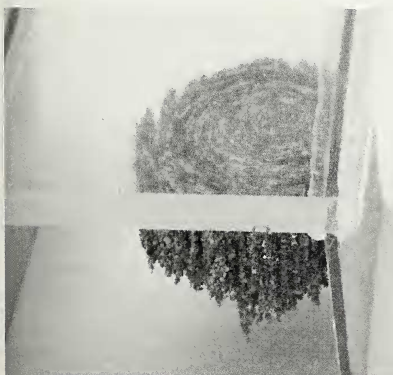


Figure 6.—Full egg sac of *Homalonychus selenopoides* showing concentric arrangement of the silk cords.

the silk threads made by males and females and the garniture of cords of silk and sand surrounding the egg sacs spun by females only occur in these spiders. We here discuss the functional role of these features and possible phylogenetic implications of their sexual behavior.

Sperm induction.—The horizontal, triangular shape of the sperm web matches what is commonly observed in spiders (Foelix 1996). The square form is also common (Gertsch 1979). We found both web forms in different sizes, but the factors that determined the shape and size of the webs were not clear to us. Although the sperm web of the sister species *H. theologus* is triangular, its area is only 2–4 mm² (Dominguez & Jiménez 2005), much smaller than what we found among *H. selenopoides*. Duration of sperm induction is consistent with observed behavior of most spiders, which require less than half an hour to perform (Gertsch 1979). The filling of pedipalps with sperm corresponds to the indirect form (Foelix 1996) and is consistent with what is commonly reported for cursorial spiders (Jackson & Macnab 1991). The alternating loading of pedipalps is similar to *Schizocosa crassipes* (Walckenaer 1837) (Lycosidae), but differs in that *S. crassipes* slowly agitates each pedipalp after loading the sperm (T. H. Montgomery in Gertsch 1979). Webs were not consumed by males, as in *Sicarius* (Levi 1967).

Induction is a common phenomenon, but observing this behavior requires patience (Gertsch 1979). Reports of induction vary from only descriptions of sperm webs (Dominguez & Jiménez 2005; Sierwald 1988), partial observations of the induction process (Fraser 1987), single observation of the entire process (Levi 1967; Jackson & Macnab 1991), and repeated observations of the entire process (Rovner 1967; Stumpff 1990). When the process takes several hours, it is easier to observe, as in some Theraphosidae (Costa & Pérez-Miles 2002). The males we studied were very sensitive to light, sound, and vibration during sperm induction and if disturbed, either ceased their activity or did not initiate it. Hence, we assume that successful observations of induction depend on its duration (Costa 1975), sensitivity of the species to surrounding environmental events, and whether the induction is unpredictable or it occurs immediately before or after pseudo-copulation or copulation.

Silk and sand threads.—We were surprised to observe males and females spinning threads of silk and sand. We noted that immature and adult specimens have their spinnerets contracted in the opisthosoma and, like other cursorial desert spiders, do not create security threads. Hence, we assume that releasing threads when males and females are searching for potential mates has a role in sexual marking. The presence of sex hormones in the threads is possible because silk is the main hormonal substrate in spiders; in other species both sexes emit and respond to pheromones (Gaskett 2007). Male silk can attract females (Roland 1984) and promote the beginning of courtship (Ross & Smith 1979). This function seems reasonable for *H. selenopoides*, because it rarely occurs in the field (unpublished data). Moreover, male silk affects courtship of conspecific males (Ross & Smith 1979; Ayyagari & Tietjen 1987). We observed that a male walking on a thread produced by another male immediately stopped and wove his own thread just above the previous one. There is no precedent in the literature for this behavior or about spiders adding sand to silk threads.

The pheromones released by females spiders as an attractant for males to induce courtship are amply documented (Gaskett 2007). However, in our study, only one virgin female spun silk threads. It is possible that the small size of the terrarium permitted pairs to meet more easily than in the field, so spinning of silk threads by females (and males) was unnecessary, and these silk threads were by-passed in favor of direct contact between partners (Dondale & Hegdekar 1973). In the field, where these spiders are uncommon, silk threads could play an important role for locating mates.

Mating behavior.—In general, mating behavior of *H. selenopoides* is similar to *H. theologus*. In both species, males usually take the initiative and approach females; however, some *H. selenopoides* females made approaches and initial contact to trigger the search or male courtship. Initiative by females for courtship was not observed in *H. theologus* (Dominguez & Jiménez 2005). Females starting courtship has also been observed in *Lycosa* spp. (Costa 1975; Rovner 1968). Although *Homalonychus* females are relatively sedentary (Crews & Hedin 2006), it is possible that, in their sexually receptive stage, they are more vagile. Active participation of both sexes in search and courtship may explain their presence in pitfall traps in the collection area. 15 of 17 *H. selenopoides* specimens trapped were adult males (47%) and adult females (53%) (unpublished data).

In *H. selenopoides*, mounting occurred on either side of the female. During copulation, the males vibrated legs II and IV, in contrast to *H. theologus*, where mounting occurred frontally and males vibrated legs II and III during copulation (Dominguez & Jiménez 2005). In both species, copulation could finish when the male ceased activity, dismounted from the female, and withdrew, but in *H. selenopoides*, there was variation in the way to end copulation. In this latter species, copulation also ends when the female suddenly spreads her legs, breaks the nuptial veil, and the male has to flee.

Courtship falls between levels I and II described by Platnick (1971), as in *H. theologus* (Dominguez & Jiménez 2005), Lycosidae, and Pisauridae. Evidently, the primary trigger of courtship or mounting behavior in the male is the direct contact with the female, but we hypothesize that males can also detect a female by a chemical stimulus. We assume that there is a contact sex pheromone in the cuticle of virgin females (Dondale & Hegdekar 1973). When males touched unreceptive and motionless field-collected females in some pairs, they did not attempt mounting. But in most other pairs, when the males touched virgin laboratory-reared females, they immediately attempted mounting. Male spiders detect pheromones by touching the females because they have tarsal receptors involved in sexual recognition (Foelix 1996). Pheromones that attract or promote the courtship of males in the female cuticle have been reported in at least 25 species of spiders (Gaskett 2007). Pheromones in *Homalonychus* and their role in sexual behavior deserve to be investigated.

Homalonychus selenopoides take the "lycosid position of copulation" (position III, Foelix 1996), similar to what is described for other wandering spiders, such as Lycosidae (Stratton et al. 1996), Pisauridae (Merret 1988), Agelenidae (Fraser 1987), Philodromidae, Clubionidae, Salticidae, and Thomisidae (Foelix 1996). Basically, in this position, males mount facing the opposite direction from the female, with the

ventral surface of the male prosoma on the dorsal surface of the female opisthosoma. In lycosids, males lean towards either side of the female to insert one or another of their pedipalps. In *H. selenopoides* this position is modified. The male places the quiescent female toward one side and then the other to insert one or another of his pedipalps, similar to the report on *Ancylometes bogotensis* (Keyserling 1877) (Pisauridae) (Merrett 1988) although in *H. selenopoides* the insertion of pedipalps is not strictly alternating. After this point, copulation is identical to that of *H. theologus* (Dominguez & Jiménez 2005).

The low frequency of sexual cannibalism observed is consistent with the claim that high frequency of cannibalism is a myth and not common among spiders (Foelix 1996). The two events of sexual cannibalism here observed are the first reported for Homalonychidae, because this behavior was not observed in *H. theologus* (Dominguez & Jiménez 2005). For the other two cases of predation upon males, these events did not represent sexual cannibalism because there was neither courtship nor copulation (Elgar 1992).

Regarding success in pairings, it is possible that *H. selenopoides* females are monandrous. This would explain the marked difference in the percentage of successful copulations between females collected in the field and the virgin females obtained in the laboratory. It is likely that most females collected in the field had already copulated since we also collected adult males.

Bridal veil.—The bridal veil is defined by Bristowe (1958) as silk threads deposited by males on females during courtship or copula. Although it occurs in species of at least 12 families, the veil of *H. selenopoides* is only identical to *H. theologus* (Dominguez & Jiménez 2005). According to the brief description of the veil of *Thalassius spinosissimus* (Karsch 1879) (Pisauridae) (Sierwald 1988), the shape and width of the bundle appear to be similar to the two *Homalonychus* spp. The extent of tying is also similar to *A. bogotensis* (Merrett 1988), but in the pisaurid, the veil is composed of an outer ring at the distal end of legs I–III and an inner ring at the level of the patellae.

Several functional hypotheses have been proposed for the bridal veil (Ross & Smith 1979; Schmitt 1992; Dominguez & Jiménez 2005; Aisenberg et al. 2008). We cannot support or refute the suggestion that the veil in *H. selenopoides* functions as a deterrent to other males during copulation. However, we doubt that the veil in *H. selenopoides* aids to identify the male as a consort because the veil is woven when the female is receptive and has become quiescent, nor do we believe that the veil restrains the female to prevent her from attacking the male or inhibit the aggressiveness of the female, as suggested for *H. theologus* (Dominguez & Jiménez 2005). We observed females that quickly broke free of the veil after copulation, ending their quiescence. The female that cannibalized her partner immediately after copulation broke out and captured him in about one second. Robinson & Robinson (1973) proposed that the main function of the bridal veil in all species that produce it is to stimulate the female. Preston-Mafham (1999) argued that courtship behavior in these species is very rudimentary, but pheromones in the veil may cause important physiological changes in the female epigynum to prepare it for insertion of the pedipalps. To fully determine the role of the bridal veil in *Homalonychus* requires further investigation.

Egg sac construction.—We have not found a precedent in another genus of spiders for garnitures of silk and sand cords surrounding the egg sac as in *Homalonychus*. Although *Sicarius* attaches sand to the wall of its egg sac (Levi & Levi 1969), it does not make a garniture of cords. Because *Sicarius* spp. inhabits deserts of South America and southern Africa (Platnick 2009), Dominguez & Jiménez (2005) suggest a convergence between the two phylogenetically unrelated genera as a response to harsh desert conditions. However, there are distinct differences in the timing and egg sac spinning process, form, and structure, and the fact that *Sicarius* spp. use their legs to bury their egg sacs with sand.

The description of the egg sac of *H. theologus* (Vetter & Cokendolpher 2000) is incomplete because it fails to mention the thick exterior garniture of cords, although in a published photograph some of them are apparent. Also, spinning of the egg sac of *H. theologus* (Dominguez & Jiménez 2005) was made at an atypical site, the side wall of the container. We infer that *Homalonychus* requires a shelter with a horizontal roof for spinning typical cylindrical egg sacs with exterior garniture of silk cords. We suggest that further study is needed to define the typical structure and spinning process of egg sacs in *H. theologus*. We agree with Vetter & Cokendolpher's (2000) and Dominguez & Jiménez's (2005) hypothesis that the sand covering the egg sac acts as a protection from predators and parasites and ameliorates the intense desert summer heat, where temperatures can exceed 45° C. We suggest that the cord garniture has this function, at least.

Phylogenetic implications.—Since the genus *Homalonychus* was described in 1891, it has remained in an uncertain phylogenetic placement (Griswold et al. 1999). Historically, researchers have hypothesized that there is a relationship with Pisauridae, Selenopidae, Zodariidae, Ctenoidea, and Pisaurioidea (Crews & Hedin 2006). Proposals based on morphology, sexual behavior, and even on molecular analysis appear insufficient to draw a stable phylogenetic hypothesis.

Courtship and mating behaviors are considered important characteristics for reconstructing phylogenetic relationships in spiders (Platnick 1971; Bruce & Carico 1988; Stratton et al. 1996). Based on the mating position, and occurrence and form of the bridal veil, Dominguez & Jiménez (2005) suggest that *H. theologus* is related to Pisauridae and could be included in the superfamily Lycosoidea of Coddington & Levi (1991). Based on morphological characters, Roth (1984) proposed retaining Homalonychidae as a separate family, criteria maintained by Coddington and Levi (1991). Griswold et al. (1999) lists Homalonychidae and seven other families as groups whose relationships in higher taxa are uncertain.

In a molecular survey, Miller et al. (2010) find Homalonychidae are very closely related to Tengellidae, but the phylogenetic placement of both families was inconsistent. Penestomidae was very closely and consistently related to Zodariidae, with all four families included in the Zodarioidea clade. The possible relationship of *Homalonychus* with zodarioids opens the possibility of finding homologies in reproductive behavior; however, the sexual behavior of Tengellidae and Zodariidae is too slightly known (Barrantes 2008; Pekár & Král 2001; Pekár et al. 2005) to make comparisons and afford a basis for considering relationships with Homalonychidae.

However, a close phylogenetic relationship does not necessarily imply similarity of reproductive behavior, and the inferred gene trees do not necessarily correspond to species trees (Nichols 2001; Degnan & Rosenberg 2009). Hence, we suggest that courtship and mating behavior could be useful in reconstructing phylogenetic relationships in spiders, complementing morphological and molecular analyses, but with careful consideration of the possibility that similar behaviors could be cases of convergence. Studies of reproductive behavior and molecular analysis of zodariids and tenebrionids (including psittacids) could help to reconstruct their phylogenetic relationships with homalonychids, as well as understand the evolution of reproductive behavior of all these little known spiders.

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